THE STATUS OF NITROGEN IN THE HAWKESBURY SANDSTONE SOILS AND THEIR PLANT COMMUNITIES IN THE SYDNEY DISTRICT. III.

The Sources of Loss of Nitrogen.

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Synopsis.

All available data relevant to the loss of nitrogen from climax communities developed on Hawkesbury Sandstone are presented. The sources of loss are erosion, drainage water, denitrification and fire. Erosion losses resulting from the natural geologic erosion cycle and fire are estimated at approximately 0·15 lb N per acre per year and are based on data of a siltation survey of a water storage dam. A lysimeter study and analysis of dam water indicate that the nitrogen content of rainwater is not completely absorbed during its passage through these communities, but that losses in drainage water are small. The results of laboratory incubation of soil suggest that denitrification occurs only in local areas of swamp where nitrate-nitrogen may frequently be detected in the surface layers of the soil. Losses due to fire are erratic, being dependent on the occurrence and severity of the fire as well as the nature of climatic conditions immediately after the fire.

The losses of nitrogen are assessed in relation to the losses of phosphorus and calcium which have occurred in the development of the sandstone communities. A comparison of the initial level of phosphorus and calcium, determined by the amounts present in the parent material, and the existing levels in the communities developed on this parent material, indicates that phosphorus has been retained to a far greater extent than has calcium. At the present time, phosphorus is the chief nutrient deficiency of these soils and it is suggested that phosphorus levels have always controlled the economy of other nutrient elements, including nitrogen, in these communities.

Introduction.

The nutrient capital of an ecosystem is a resultant due to the operation of factors which are contributing to and removing from it. The capital of nitrogen in Hawkesbury Sandstone communities has been calculated in earlier papers (Hannon, 1956, 1958) and the factors concerned in the removal of fixed nitrogen in these communities will now be discussed.

A loss of nitrogen from a plant community may occur by any of several possible routes. These may involve factors resulting in the loss of nitrogen from one stand and its redistribution in other areas, or an absolute loss of nitrogen from the earth's surface to either the ocean or the atmosphere. Either mechanism causes a loss from any particular stand. They may involve the removal of nitrogen-containing soil particles by wind or water erosive forces; the solution and removal of nitrogen in drainage waters; or the mechanism of absolute loss—the change from a combined state of nitrogen to a free gaseous form and its release to the earth's atmosphere. It is obvious that a certain loss is of probable occurrence in the majority of ecosystems, but the magnitude of losses will depend on the nature of the ecosystem. The factors operating to allow loss of nitrogen from the Hawkesbury Sandstone ecosystem are erosion, drainage water, denitrification and fire.

1. Erosion.

Presentation and Discussion of Data.

No direct measurements of the removal of soil particles have been made, but field observations allow at least a qualitative assessment of this source of loss. On the plateau, soil and weathered particles from rock outcrops are exposed to wind action on

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the flat-topped dividing sectors between the valleys. Nevertheless, where plant cover occurs, it is quite dense and shows marked reduction in height and increase in density in increasingly exposed situations, and thus protects the soil.

It therefore is probable that a far greater source of erosion is the water run-off down the sides of the steep valley slopes. The general physiography of the Hawkesbury Sandstone region—the narrow, flat-topped ridges and the youthful steep gullies—indicates that a natural loss of soil particles by water erosion must be occurring to allow for the normal geological erosion cycle. Since natural erosion on a geological time scale is a very slow process, the lack of exposure of plant root systems is of no significance in assessing the extent of erosion. Soil depth is shallow on the ridges and especially on the upper slopes of the gullies; there is a marked improvement in comparison to these sites in the lower portions of the gullies which benefit by the accumulation of soil, water and nutrients from the surrounding uplands.

The only quantitative information that exists on the rate of erosion in these areas is a few data obtained by the Metropolitan Water, Sewerage and Drainage Board on the amount of sedimentation occurring in the water reservoirs. This constitutes a

TABLE 1.
Data Relevant to Silt Accumulation in the Bargo Weir in 1956.
(Taken from records of Metropolitan Water, Sewerage and Drainage Board.)

Age. (year.)	Catchment Area. (sq. mile.)	Surface Area. (acre.)	Original Capacity. (gal.)	Present Capacity. (gal.)
67	29	17	67,246,093	52,764,062

Note.—The height of the outlet pipe above the foundation level is five feet, but this has never been used. Water is drawn from near the surface by means of a trunnion pipe.

certain measure of the erosion that is occurring, but sets only a minimum value. It represents the resultant loss from a large area within which several plant formations occur. Differing amounts of soil will have been lost from different formations and, in certain of them, some re-deposition of soil particles may have occurred. Nevertheless this over-all average value of the loss of soil particles from large areas is admirably suitable for inclusion in this general survey.

The storage system providing for the Sydney water supply consists of a series of dams built on the rivers in the areas where Hawkesbury Sandstone outcrops. The construction of the dams has necessitated the building of access roads, but in order to maintain the purity of the natural precipitation, a minimum of disturbance has occurred in the catchment areas. Virgin forest covers these areas which are the private property of the Water Board. Erosion of soil particles will thus be occurring within these areas at a rate which is very similar to the natural rate. The dams, however, are of relatively recent construction (ranging in age from 1 to 55 years), and since silt accumulation has as yet provided no inconvenience, no investigation has been made of this factor. This, however, does not necessarily imply that the rate of silting is negligible, since calculations from information supplied by the Water Board show that very large quantities of soil would need to accumulate before causing difficulty.

The only survey that has been made is in the Bargo Weir situated on the Nepean Ramp about sixty miles south of Sydney. The Metropolitan Water, Sewerage and Drainage Board took control of this weir only in 1956 and the catchment area had been subject to greater biotic influences than are allowed on their other properties. Examination of aerial photographs of the catchment area reveals that 13% of the total area has been cleared; of this area, 4% is used for mixed farming. This is entirely confined to the ridges on the extreme edge of the catchment area and therefore will not have influenced the quantity of silt accumulated in the weir to a very great extent. The data supplied by the Water Board are shown in Table 1.

The loss of 14,482,031 gallons' storage capacity (Table 1) is equivalent to a volume of 2,323,780 cubic feet of silt. On the basis of an apparent density of 81 lb per cubic foot (since only surface soil will have been eroded and formed the silt), it may be calculated that this volume of soil has a mass of 188,226,180 lb. Since only the shallow uppermost layer of soil which has the highest nitrogen content would be removed by natural erosion, an apparently high value of 1,000 p.p.m. nitrogen (Hannon, 1956) will be assumed as the nitrogen content of this layer. On this basis, 188,226 lb of nitrogen has been lost over a period of 67 years from an area of 29 square miles. It is thus readily calculated that this loss corresponds to 0·151 lb of nitrogen per acre per year.

Brown (1943) and Kittredge (1948) provide figures of the quantity of soil eroded from virgin areas. Apart from one value of 1·38 cubic feet per acre per annum in mature oak forest, their values are very much less than the calculated value of 1·87 cubic feet per acre per annum for the sandstone forest.

Since many factors—such as climate, nature of the soil slope and vegetative cover—are known to influence erosion, widespread values are to be expected in different areas. In particular, the coarse texture and single grained structure of the sandstone soils and the steep slopes of the valley sides would favour erosive action. It is also worthy of note that fires are of common occurrence in the sandstone areas. Brown (1943) has shown that yearly erosion from burned areas ranged from 22 to 239 times that of unburned. The remarkable adaptations exhibited by the native species to withstand fire would indicate, however, that it is a natural occurrence in these communities.

2. Drainage.

Introduction.

The nitrogen content of drainage water is frequently investigated and stressed as a serious source of loss from cultivated fields. Where readily available forms of mineral nutrients are added to the soil in fertilizer treatment, considerable losses by this means are to be anticipated. In natural communities, similar losses would not be encountered, especially in Hawkesbury Sandstone areas where nitrogen—especially available nitrogen—is at low levels. In addition, in natural communities, drainage water can originate only from precipitation of which a certain fraction is absorbed by the soil and plant cover. Natural precipitation is a well-recognized source of fixed nitrogen; the question of greatest significance for the present purpose, therefore, becomes whether or not the drainage water, after passage through the soil, has a higher nitrogen content than the precipitation.

Lysimeters—arrangements whereby drainage waters which have percolated through a soil column are collected—are of various designs, but may be classified according to the principle of their construction into three main types—monolith, Ebermayer and filled-in varieties. Difficulties, such as (*a*) artificiality of the base, (*b*) failure to delimit the drainage area, and (*c*) disturbance of the soil block, apply to one or other of these designs and hence none is entirely satisfactory. The use of an abnormal lower surface is a serious criticism of all types of lysimeters, since gravitational water at this point has to overcome the resistance caused by surface tension at the soil/air interface before it can drain away. A waterlogged condition in this position causes many changes in the soil and influences the chemical composition of the percolate.

Method.

The least departure from natural conditions was considered an essential requirement in the present study. The principle of the Ebermayer lysimeter, where the soil is left *in situ*, was therefore followed. In this type of lysimeter, no side walls separate a definite soil block from the adjoining soil. However, by selecting areas of appropriate position and slope, it is possible, in the sandstone communities, to delimit by eye the area from which drainage waters would be collecting and in which lateral movement would be most improbable. In such areas, the naturally occurring sandstone underlying the soil mass can be used for the base of the lysimeter block, since it is less pervious to water than is the soil derived from it.

The edge of a narrow plateau region, adjacent to a steep gully, was selected for this study; this area, including the highest point of the ridge, was of gentle slope (1/12) and of 74 feet length, 10 feet width and averaged approximately 1 foot in depth (ranging from 0 to 2 feet). No waters from higher land fell onto this area which supported low scrub forest.

Soil was cut away at the lowermost edge of the selected area to uncover the underlying sandstone. A graded groove was cut in the stone to direct the flow of the water which would accumulate from the higher level. A metal sheet covered the groove and the earth was replaced over it. Thus the only disturbance was made at the point where the water was collected. The area through which the drainage water percolated remained completely undisturbed. The water flowed from the groove in the rock via a length of pipe into a funnel where it was filtered, passing thence through cationic and anionic exchange resin columns and thence into a collecting drum which contained

TABLE 2.
The Adsorption of Ammonia from Rainwater by Hawkesbury Sandstone Soil.

Ammonia Content (p.p.m.).		Ammonia Adsorbed by Soil. (%)
Rainwater.	Drainage Water.	
0·29	0·20	31
0·27	0·20	26
0·05	0·04	20
0·20	0·16	20

1½" depth of paraffin. This arrangement for the collection of drainage waters fulfilled its purpose very satisfactorily. The ammonia and nitrate and nitrite content of the percolate was concentrated on the resin columns which were renewed at intervals. On these occasions, the volume of water collected in the drum, which had been shielded to prevent evaporation, was measured and discarded.

Presentation and Discussion of Data.

There is no certainty that the total amount of drainage water from this area was collected. Some of the drainage water may have been absorbed by the sandstone, some may even have been lost through cracks in the underlying rock, but the aim of the present study, unlike many lysimeter studies, was not concerned with the quantity of drainage waters. A measure of the relative nitrogen content of precipitation and drainage water was the information required. This information would indicate whether a positive or negative nitrogen balance results from these two opposing factors in the sandstone communities.

A parallel study was therefore made of the rainwater and drainage water nitrogen content, and the results for the ammonia content of each are shown in Table 2.

A survey of the literature concerned with the nitrogen content of drainage waters shows that nitrate is the most common form—in fact, some investigators analyse only for nitrate. Ammonia, where present, is usually in only small amounts. However, lysimeter investigations are most frequently made in cropped soils where fertilizer additions are applied. Neither nitrite nor nitrate was detected in drainage water on any occasion. During this period, a similar condition applied to the rainfall and will be discussed in that connection in a later paper.

The quantity of nutrients in drainage water will depend on such a complex of factors—nature of the soil, vegetation cover and climatic conditions—that comparison with unrelated circumstances serves little useful purpose. However, in virgin bunchgrass on silty clay loam, where nitrogen is regarded as the principal limiting nutrient, Kardos (1948) records that the concentration of total nitrogen over a period of three years was consistently of the order of 2–3 p.p.m.

Table 2 shows that appreciable quantities of the ammonia content of the rainwater had been absorbed by passage through a relatively small soil block. In addition, it is most improbable that all of the drainage water had passed through all of the soil—rain falling on the lower edge would have passed through only a small fraction of the soil block.

The water stored in the dams of the Metropolitan Water, Sewerage and Drainage Board consists of surface run-off and drainage from large tracts of sandstone country. The analytical data of the composition of dam water sampled at one foot depth at monthly intervals were therefore consulted. This showed that free ammonia, albuminoid ammonia and nitrate are consistently present in these samples and nitrite very occasionally.

As is to be expected, variation is marked between dams with respect to the absolute amount of each fraction at any given sampling time; variation is also great at different sampling times; nevertheless, the values are consistently low for all nitrogenous fractions. 0·1–0·2 p.p.m. nitrogen are usual values for albuminoid ammonia and both free ammonia and nitrate usually vary between 0 and 0·088 p.p.m. nitrogen.* These values will not necessarily represent accurate values for soil leachate water nitrogen content, since dam water consists of drainage water and a small percentage of rainwater, together with surface run-off, which introduces soil particles (see silt accumulation above) as well as organic material from the litter layer. In view of the data in Table 2 and the low nitrogen content of the dam water, it appears that losses of nitrogen in drainage water reduce the nitrogen contribution made by rainfall to only a small extent.

3. Denitrification.

Method.

A typical stand of low scrub forest dominated by *Eucalyptus haemastoma*–*E. gummifera* and the edge of a shrub swamp dominated by *Hakea teretifolia* were selected as soil-sampling sites for investigations of microbial activity with respect to nitrogen transformations. Soil bags, containers and sieves had been sterilized and the spades thoroughly disinfected. A composite soil sample of about 10 kilograms was taken to a depth of 8″ in approximately 1 kilogram portions from ten sites within each stand. To avoid undue exposure of the soil to the foreign atmosphere of the laboratory, both samples were sieved and thoroughly mixed in the field before being placed into sterile containers for transport to the laboratory. Only three days elapsed from the time of sampling to the time of commencement of incubation.

100-gram portions of soil were weighed into sterile 250 ml. conical flasks for aerobic and 150 ml. flasks for anaerobic treatment. The flasks contained either (i) distilled water or (ii) a nitrogen-free mineral solution (Hannon, 1956) or (iii) 1% glucose solution or (iv) 1% glucose in the nitrogen-free mineral solution, to provide a 25% moisture level.

Each treatment was set up in duplicate and under aerobic and anaerobic conditions. In the case of the aerobic treatment, the flasks were plugged with rubber bungs fitted with both a stopcock tap and also glass tubing bent to form a double trap which contained 2N sulphuric acid and methyl red indicator. Acid in this concentration does not cause desiccation of the internal atmosphere. Any ammonia contained in air moving inwards from the external atmosphere would be fixed in the outer trap and ammonia diffusing outwards from the incubation vessel would be fixed in the inner trap. The stopcock was inserted to allow air to be drawn out of the flasks through the acid traps at the conclusion of the experiment.

The anaerobic flasks were plugged with bungs fitted with an inlet and an outlet glass tube, both of which were drawn out to narrow diameter towards their outer extremities. Within these flasks were placed: (i) a tube containing sulphuric acid and methyl red

* Visual methods of comparison of the colours of standard and unknown solutions are employed in the Water Board laboratories. The accuracy of the absolute values is therefore open to question, since visual methods are not so reliable as those employing a photo-electric cell. Undoubtedly, however, the low order of the values is correct.

suspended by enamelized wire from the bung, (ii) a bottle of steel wool which had been dipped in copper sulphate solution. As the steel wool rusted, it used any remaining traces of oxygen in the flask (Parker, 1955), (iii) a bottle of an alkaline solution of glucose and methylene blue to indicate when anaerobic conditions had been attained.

Each flask was evacuated and filled with nitrogen free of carbon monoxide, oxygen and ammonia. The nitrogen passed through a cotton plug which acted as a filter. This procedure was repeated until the methylene blue decolorized. The outlet tube was then sealed with a hand torch. The pressure within the flask was then reduced. Carbon dioxide was produced externally with a measured volume of sulphuric acid reacting with sodium carbonate to provide 5% of the volume of the flask atmosphere. By opening the evacuated flask to the chamber where the carbon dioxide had been produced, the gas was drawn into the flask, nitrogen was flushed through to restore atmospheric pressure and the inlet tube also sealed.

TABLE 3.

The Total Nitrogen Content of Hawkesbury Sandstone Soils before and after Incubation under Conditions of Darkness.

Soils were incubated for 12 weeks, with various nutrient additions at 25 °C. and with an initial moisture level equivalent to field capacity.

Soil Sample.	Gaseous Treatment.	Nutrient Treatment.	Total Nitrogen Content (p.p.m.).	Change in Nitrogen Content.
Forest.	Aerobic.	Non-incubated.	580	Initial value.
		Control (+water).	560	Not significant.
		N-free minerals.	570	Not significant.
		1% glucose.	565	Not significant.
		Glucose+N-free minerals.	560	Not significant.
	Anaerobic.	Control.	580	Not significant.
		N-free minerals.	585	Not significant.
		1% glucose.	600	Not significant.
		Glucose+N-free minerals.	600	Not significant.
Swamp.	Aerobic.	Non-incubated.	690	Initial value.
		Control.	590	16% loss.
		N-free minerals.	590	16% loss.
		1% glucose.	610	12% loss.
		Glucose+N-free minerals.	600	14% loss.
	Anaerobic.	Control.	620	11% loss.
		N-free minerals.	600	14% loss.
		1% glucose.	580	17% loss.
		Glucose+N-free minerals.	570	19% loss.

Both aerobic and anaerobic treatments were incubated in darkness for twelve weeks. Analyses were made by the Kjeldahl method (Hannon, 1956) to determine differences in the initial and final total nitrogen content of the soil samples.

Presentation and Discussion of Data.

The results in Table 3 show that no fixation of nitrogen occurred in either sample under these experimental conditions. In addition, although no loss occurred in the forest sample, significant losses of nitrogen occurred in all treatments of the shrub swamp soil. Apparently the aerobic treatment contained local patches of anaerobic conditions which prevented distinction between the aerobic and anaerobic conditions employed. The losses of nitrogen in the swamp soil are of interest, since it has already been shown (Hannon, 1956) that the swamps generally have a higher total nitrogen content than the forest soils; in addition, in a bio-assay trial, more nitrogen became available in the swamp samples.

At the conclusion of the incubation, in no instance was ammonia detected in the acid traps in quantities of even 10 micrograms. The observed losses were of the order of 10,000 micrograms and apparently occurred in the form of elemental nitrogen or as an oxide of nitrogen.

Wijler and Delwiche (1954) have shown that nitrous oxide is the usual form of nitrogen loss under most soil conditions, but where the environment is strictly anaerobic, only molecular nitrogen is lost (Jones, 1951). Except in instances where ammonium and nitrite have been added at levels which probably never occur in natural soils (Ingham, 1938; Fraps and Sterges, 1939; Wahhab and Fazal-Uddin, 1954) denitrification has been shown to be due to bacterial activity. Denitrification occurs only in the presence of nitrogen in an available form and in the absence of oxygen from the soil solution (Jones, 1951; Skerman, 1953; Arnold, 1954).

It therefore appears that the losses occurring under incubation conditions in swamp soils may very probably occur in these habitats in the field. Available nitrogen is at very low levels in sandstone soils, but in swamp areas nitrate is frequently detected in the surface layers. The presence of free water would assist in the development of anaerobic conditions. Nothing is known of the availability or of the carbon-nitrogen ratio of the oxidizable water soluble substances which provide the necessary substrate for the activity of the appropriate bacteria. However, since nitrogen losses occurred in the control treatment of the incubation series, the naturally occurring organic matter apparently furnishes a suitable substrate. Some character of the soil from the sclerophyll forest areas must prevent the occurrence of denitrification—lower levels of nitrate and naturally occurring organic matter may be suggested.

4. Fire.

Discussion.

The destruction of organic matter as a result of fire causes a potential loss of nitrogen and mineral constituents from the nutrient capital of the ecosystem—from the vegetative cover, the litter and in some instances from the surface layers of the soil. The charred remnants and ash are left exposed to the erosive forces of the environment.

In the sandstone communities, while all but the heaviest of the woody material is burnt, most of it is only charred and allows for the early commencement of regeneration. A fine deposit of ash is left covering the ground surface and floating in the atmosphere in the wake of the fire. In local patches where fallen logs have smouldered, distinct areas of ash deposits are to be found. The ash is very readily disturbed and usually is completely removed soon after the fire. The extent of loss depends on the nature of the environmental conditions immediately after the fire. The ash is largely derived from the foliage of the shrub layer. In forest areas, the leaves of the trees often are only scorched and drop soon after the fire. This litter layer often assists in the protection of the ash lying on the bared ground surface. Regeneration by way of seed, lignotubers and epicormic buds probably draws largely on stored food reserves, but in such periods of active growth, nutrient absorption by the root systems from the temporarily enriched soil could well occur and incorporate the ash components once again into living tissue.

Certain losses of nutrient capital undoubtedly occur as a result of fire and the cumulative effect of the countless fires that must have occurred since the establishment of plant communities on Hawkesbury Sandstone could well be considerable. It is probable that no stand occurring on Hawkesbury Sandstone can be regarded as "fire-free". The remarkable protective adaptations of the flora against fire suggest that fire occurrence predated and may possibly have contributed to the selection of the present flora. Fire cannot therefore be regarded as a completely unnatural phenomenon in these communities. It may be that the present-day communities are not equivalent to the original cover because, amongst other factors, the nutrient capital has been depleted. However, as far as can be judged in the absence of fire history records, the marked differences that often occur between various stands of the same formation could well be related to local environmental differences, such as wind exposure, moisture level or the stage of regeneration from fire, rather than the past history of firing. Field observations of fully regenerated stands indicate either that the losses are made up or that the loss as a result of fire is insignificant.

Hatch (1959) has found that in fire-breaks within *Eucalyptus marginata* forest in Western Australia, controlled burning at 1–3 year intervals has not significantly influenced the properties, including total nitrogen content, of surface (0–3½″) soils by comparison with adjacent forested soil protected from fire for 15–25 years.

Reports regarding the effect of fire on soil nitrogen are contradictory (Ahlgren and Ahlgren, 1960). Increased nitrification rate has often been reported due to the effect of the changed pH on bacterial growth. Such changes represent only a redistribution of the total capital of nitrogen in the soil. Absolute losses of nitrogen as in a stimulated rate of denitrification have also been reported, but further investigation of these aspects is required.

Certain compensation for the losses caused by fire will result from the slow but continual weathering of the outcropping parent material. In addition, the heat of the fire frequently causes fretting of superficial layers of the sandstone, thus releasing ash components and making further nitrogen fixation possible.

TABLE 4.
A Comparison of the Phosphorus and Calcium Content of Hawkesbury Sandstone and Sandstone-Derived Soil.

	Total P Content.*			Total Ca Content.*		
	Hawkesbury Sandstone. (p.p.m. P.)	Soil. 0–6″ (p.p.m. P.)	Soil. 6–40″ (p.p.m. P.)	Hawkesbury Sandstone. (p.p.m. Ca.)	Soil. 0–6″ (p.p.m. Ca.)	Soil. 6–40″ (p.p.m. Ca.)
Average	29	30	24	307	33	18
Range	15–38	22–34	16–37	215–430	9–48	9–27

* P analyses are based on 8 samples, Ca analyses on 5 samples. Calcium analyses of the sandstone were made at the School of Mining Engineering and Applied Geology, University of New South Wales, and calcium analyses of the soil are from Storrier (1951).

Losses of nitrogen due to fire cannot be denied and their significance is difficult to assess. However, the fractionation of nitrogen in the Hawkesbury Sandstone ecosystem (Hannon, 1958) shows that the main bulk of nitrogen is contained in the soil and woody tissue of the plant cover and this will be practically unaffected by fire.

An Assessment of the Losses of Nitrogen.

The nitrogen content of the Hawkesbury Sandstone ecosystem has obviously been derived from external sources rather than the parent material (Hannon, 1956). Many factors may have contributed and caused losses in the development of the nitrogen capital of the present-day community. Consequently, it is impossible to estimate quantitatively or with accuracy the extent of the contribution or of the removal caused by each factor since the first plant colonization of Hawkesbury Sandstone. A statement concerning the absolute losses of nitrogen from the combination of all possible sources of loss is therefore not possible.

However, by the time the ecosystem attains maturity, an equilibrium value has been reached for the content of each nutrient element in organic form. This is the amount which can be actively used under the conditions of the existing environmental complex. Instances of luxury consumption of certain elements would prove exceptions to this statement, but are unlikely to be relevant in the case of most nutrient elements in Hawkesbury Sandstone communities, where the parent material contains only very low concentrations of the elements required for the growth of living organisms.

Since the incorporation of nitrogen into an ecosystem, at least by biological means, is dependent on the supply of other mineral elements to allow the development of the appropriate organisms, a consideration of the losses of other nutrients, whose amount in the ecosystem is determined initially by the amount in the parent material, will be of relevance to the assessment of the losses of nitrogen.

Phosphorus and calcium have therefore been selected, since it has already been shown that phosphorus is the primary nutrient deficiency of these communities (Beadle. 1953, 1954; Hannon, 1956) and calcium levels in the sandstone soils are very low. The significance of calcium to biological nitrogen-fixing agencies is well known. Analytical data of Hawkesbury Sandstone, sandstone-derived soils, plant tissue and litter of the sandstone species are relatively few in number and have frequently been made by different workers on samples collected in different areas.

Hawkesbury sandstone and soil derived from sandstone taken from the same area are compared with respect to their phosphorus and calcium contents in Table 4. Where comparison is to be made between the nutrient contents of the solid parent material and of the porous soil derived from it, a concentration or mass basis must be used rather than a volume basis. It appears that the mineral content of the parent material has been retained in the soil to a greater extent in the case of phosphorus than of calcium. Even without the addition of the phosphorus content of living plant tissue and litter, it is obvious that the initial phosphorus content has been largely retained in the present-day communities. However, on the basis of measurements and observations recorded previously (Hannon, 1958) and unpublished analytical data of Beadle, Winterholder, Fraser (1948) and Turner (1954), a calculation relating the calcium content of the Hawkesbury Sandstone to that of soil, plant tissue and litter indicates that only 20% of the calcium contributed from decomposition of the sandstone can still be accounted for.

Presumably the leaching action of drainage waters over long periods of time has caused the losses of calcium during the development of the present-day sandstone communities. Erosion losses cannot be considered as contributing to this loss to the same extent, since a given quantity of soil is compared with a similar quantity of parent material.

It may be suggested that a severe limitation to plant growth set by the phosphorus level may have prevented the uptake and utilization of calcium. Similarly, it may be suggested that the accretion of nitrogen by biological agencies would also have been limited by the phosphorus level, and that nitrogen fixation has proceeded at a rate in pace with the rate of phosphorus liberation from the parent material. Under these circumstances, excess quantities of nitrogen would never have occurred and consequently never provided a source for loss. If denitrification has occurred, loss of nitrogen by this means is not accompanied by a loss of phosphorus and therefore a counterbalancing gain of nitrogen by fixation could occur. Because of the necessity for particular environmental conditions for its occurrence, denitrification probably has always been confined to swamp areas, which may have been more extensive in the past.

In fires, where the loss of nitrogen will be relatively greater than that of phosphorus, a similar counterbalancing gain of nitrogen by fixation might be anticipated.

Losses of nitrogen due to losses of soil by natural erosion in these communities must also be accompanied by losses of phosphorus and other nutrient elements. Such losses therefore do not result in the relative depletion of the remaining soil in the same manner as does, for example, denitrification, where nitrogen alone is lost. It is well recognized, however, that the upper layers of the soil which are removed by erosion are the most fertile, especially with respect to nitrogen (Ensminger and Pearson, 1950). Of all sources, erosion probably has caused the greatest loss of fixed nitrogen from these communities.

On these grounds, it appears that the nitrogen economy of these communities is controlled by an efficient phosphorus regime. Erosion, leaching, denitrification and fire all play a role in some phase of the sandstone communities. Unless factors are operating to counterbalance these losses, deterioration of the communities must ensue. Studies reporting the occurrence and activity of agencies capable of contributing nitrogen to these ecosystems will be reported later.

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